VEGETATIVE VIGOR OF THE HOST AS A FACTOR INFLUENCING SUSCEPTIBILITY AND RESISTANCE TO CERTAIN RUST DISEASES OF THE HIGHER PLANTS

II

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Further Field Studies and Experiments

The Rust History of Plots of Cereals Sown at Successive Intervals through the Summer

To test the susceptibility to rust of plants of different ages at each period of the summer and of young plants at different times in the summer, and to follow the subsequent history of the disease on plantings of cereals started at successive intervals through the season, plots of wheat, rye, oats, and barley were started in the breeding plot of the New York Botanical Garden on June 10, June 23, July 6, July 20, August 5, and August 25, 1916. Observations were made at intervals on the height of the plants, the time of first appearance of the rust, the amount of infection, and the proportion of the rust in the teleuto stage.

The results for the different cereals are shown in table 3 and are discussed below. In the table, the days on which the observations were made are given at the top. The height of the plants is given in inches (″). When the plants have headed, it is indicated by an "H." The degree of rust infection is indicated by a numeral, and was estimated on a scale of 10, the values of the numbers in the scale being: 1 = an occasional pustule here and there; most of the leaves not affected. 2 = most of the leaves with from one to five sori. 3 = about ten pustules on each leaf. 4 = leaves heavily infected. 5 = leaves bearing the maximum possible amount of rust. 6 = leaf sheaths infected as well as the leaf blades. 7 = a sprinkling of rust sori on the stem and leaf sheaths; blades heavily infected. 8 = infection on sheath and stem well developed. 9 = heavy infection on the stem. 10 = heaviest possible infection on the whole plant. The teleuto stage is indicated by its Roman numeral, "III." A fraction preceding the "III" gives the proportion of the rust in the teleuto form.

As is indicated in table 3, the plots of wheat planted on June 10 and June 23 headed out in 77 and 64 days respectively. Those planted July 6, July 20, August 5, and August 25 never headed and never exceeded a height of 20 inches. The rust invariably appeared on the young plot as a thin, evenly distributed infection when the host plant was putting out its

TABLE 3

Wheat

Date Sown	Observations								No. of Days to Head
	July 8	July 17	July 24	Aug. 12	Aug. 26	Sept. 15	Oct. 1	Oct. 23	
June 10...	8″–2	12″–4	18″–4	24″–5	H–6	7	7 slight III		77
June 23...	2″	9″–2	12″–4	20″–4	H–5	6 slight III	7 slight III	6 slight III	64
July 6....		5″	8″–1	15″–5	18″–5	18″–5	20″–5	20″–4	
July 20...				10″–3	12″–5	15″–4	20″–5	20″–3	
Aug. 5....					9″–3	10″–4	15″–5	15″–4	
Aug. 25...						5″–2	9″–4	15″–3	

Rye

Date Sown	Observations								No. of Days to Head
	July 8	July 17	July 24	Aug. 12	Aug. 26	Sept. 15	Oct. 1	Oct. 23	
June 10...				de- stroyed					
June 23...	3″	9″–2	20″–2	H–3	4	7	7	7	33
July 6....		5″	8″–1	15″–3	H–5	6	7	7	51
July 20...				6″–1	12″–4	18″–6	H–7	6	73
Aug. 5....					4″–1	10″–5	15″–6	H–5	79
Aug. 25...						8″–2	10″–5	20″–4	

Oats

Date Sown	Observations								No. of Days to Head
	July 8	July 17	July 24	Aug. 12	Aug. 26	Sept. 15	Oct. 1	Oct. 23	
June 10...	10″	14″	18″	H–2 slight III	6 slight III	8 ¾ III	9 all III		77
June 23...	5″	10″	18″	24″–2 slight III	H–7 ½ III	8 ¾ III	9 all III	9 all III	63
July 6....		4″	8″	15″–2 slight III	20″–6 slight III	H–8 ⅔ III	8 ¾ III	8 all III	70
July 20...				10″–1	12″–3 slight III	18″–5 ½ III	24″–6 ⅔ III	H–8 ¾ III	91
Aug. 5....					9″–1	15″–5 slight III	18″–5 ¼ III	20″–7 ¾ III	
Aug. 25...						6″–1	10″–2	15″–5 ⅓ III	

Barley

Date Sown	Observations								No. of Days to Head
	July 8	July 17	July 24	Aug. 12	Aug. 26	Sept. 15	Oct. 1	Oct. 23	
June 10...	8″	15″	H			2	1		44
June 23...	4″	15″	18″	H		1	3		50
July 6....		3″	8″	15″	H		1	1	50
July 20...				9″	15″	20″	H		70
Aug. 5....					6″	10″	15″	15″	
Aug. 25...						6″	10″	12″	

third leaf. The rust increased steadily in abundance on the leaf blade until it reached the maximum, and only then began to appear on the leaf sheaths. On the stem there were never more than a few scattered pustules. Teleutosori did not appear until the middle of September. They were to be found only on plants of the two oldest plots, and then not without careful search. The observations of October 23 showed a distinct drop in the amount of rust on all the plots of wheat. The new leaf growth of October tended to show but little rust. In view of Johnson's (1912) findings that low temperatures promote uredospore germination, these observations may be interpreted as indicating greater resistance to rust infection on the part of the host tissue due to the decreased rate of metabolic activity consequent on the onset of cooler weather.

All of the plots of rye except that sown August 25 headed out, but the rate of growth varied as is indicated by the successively greater intervals required by the younger stands to head out. The behavior of the rust on the plots of rye was much the same as on the wheat. In the younger plantings it was somewhat less marked and less severe than on the wheat plants of the same age, but the development of the rust was more severe on the rye than on the wheat. It seemed, too, to go more readily to the leaf sheaths and stems in the case of the rye. No teleuto was found on the rye.

Of the oats, the first three plots headed out in 77, 65, and 70 days respectively; the fourth plot produced only one head, 91 days after planting. The plots planted August 5 and August 25 never headed out. No rust appeared on the oats until August 12 when four plots were up, ranging in age from seedlings in the four-leaf stage to plants in bloom. The rust appeared on all four of the plots at the same time and in relatively the same abundance. However, once the rust had appeared, its subsequent history on the various plots differed decidedly. The older the plant, the greater the abundance of rust on it, and the larger proportion of the rust in the teleuto stage.

In the series of barleys, the three older plots headed in 42, 50, and 50 days respectively. The fourth put out a few heads 70 days after planting.

The last two sowings, of August 5 and August 25, never reached the heading-out stage. The barleys were rust-free until the middle of September, when a few uredo pustules were to be discovered on the leaves and sheaths of the three older plots. No teleuto was found.

As has been noted for the plots of wheat and rye, even more strikingly in the case of the oats, the rate of development of the parasite differs with the host. It is much more rapid in the case of the oats than in that of the other cereals. For example, in the seedling stage the amount of rust on the plants may appear less on the oats than on the rye and wheat, although at the time of heading out the same plants will show the reverse condition, the oats being much more severely infected.

The rust history of plots of cereals sown at successive intervals through the summer may be taken as indicating that the age and maturity of the host is a factor in the progress of the disease, and that the action of this factor differs with the identity of the host plant.

Laboratory and Greenhouse Studies

Culture Methods

Four cereal rusts—*Puccinia coronifera* Kleb., *P. secalina* Grove, *P. triticina* Eriks., and *P. Sorghi* Schw.—were successfully grown for periods of time on the host in pots on greenhouse benches as described by Melhus (1912) and Fromme (1913), and under aseptic conditions on host seedlings growing in test tubes as described by Ward (1902*a*) and Mains (1917). Variations were introduced in both methods.

Fromme (1913) reviews the problem of growing cereal rusts in the greenhouse. The method recommended by him includes sowing rust spores on new host plants every few weeks by applying them with a scalpel or camel's hair brush, or spraying on in suspension in water with an atomizer, and then putting the host plants into a moist chamber for from 24 to 48 hours to provide the conditions of high humidity necessary for spore germination and infection. Tests, however, indicated that the first part of the method recommended by Fromme, artificially sowing rust spores on the new host, was not necessary under the conditions obtaining in the Columbia greenhouse. It was found that when new host plants are grown beside infected plants in the greenhouse, rust spores will be sown on them by natural agencies, such as convection and other atmospheric currents, sufficient to produce abundant infection if conditions of high humidity are provided occasionally to render possible the germination of the spores.

Accordingly, the method adopted for maintaining stock cultures of the cereal rusts in the greenhouse was to introduce new host plants alongside the infected plants every third week and to cover the cultures with a moist chamber every second or third night. The fungus maintained itself self-sown in this manner, and no artificial inoculations were needed. The

advantage of such a method of maintaining stock cultures of cereal rusts is that it eliminates the most technical operation, that of sowing or applying the fungous spores to the new host, and reduces the problem of maintaining cereal rusts in culture in the greenhouse to a non-technical routine such as can be entrusted to the average gardener or greenhouse man.

In growing the rust under aseptic conditions on seedlings in test tubes, the method developed was to treat the seed with chlorine water (*cf.* Wilson, 1915), put the seed to germinate on filter paper in Petri dishes, and transfer the germinated seed to a test tube plugged with cotton. Half an inch of sterile water was put into the test tube with the plant. The reserve food materials of the endosperm are capable of bringing the seedling to the third leaf stage, which is sufficient to raise a generation of the rust on it. *P. coronifera* was cultivated for 10 generations in this manner, transfers being made once a month; *P. Sorghi* for 8 generations; *P. triticina* for 8 generations; and *P. secalina* for 6 generations. A small platinum spatula was employed for making transfers; spores were applied to the upper surface of the first leaf in each case, and material for inoculum was taken from the under surface. That a cereal rust can thus be grown under conditions free from accidental contamination was indicated by the total absence of organic growth, bacterial or fungous, when a rust-infected seedling was deposited on sterile beef-peptone agar.

Studies on the Incidence of Infection by Measured Doses of Uredospores of Puccinia Sorghi on Zea Mays

An effort was made to determine the minimal dose of uredospores of *P. Sorghi* that (1) can possibly, and (2) will certainly produce infection in *Zea Mays.* 191 tests were made on corn seedlings growing under aseptic conditions in twelve-inch test tubes.

The method employed to determine the dose and to inoculate was as follows: A dilute suspension of uredospores was made in a vial of sterile water. A small drop from this suspension was put on a piece of sterile cover slip, and the number of uredospores in the drop was counted under the microscope. The piece of cover glass was then inverted and deposited on the upper surface of the first leaf of the young corn seedling in the test tube, about one half inch below the tip, bringing the drop of water containing the known number of uredospores in contact with the host tissue. The work was done in the winter in the laboratory, with no rust growing free anywhere in the building, so that the danger of accidental contamination was negligible. No infection ever developed on the seedlings except on the spot where the plant had been inoculated.

The inoculated seedlings were kept under observation for 21 days. If the inoculated leaf yellowed or withered before 15 days, the plant was discarded. The data on 191 tests are shown in table 4.

TABLE 4

No. of Spores	No. of Inoculations	No. of Infections	No. of Spores	No. of Inoculations	No. of Infections
1	58	2	52	1	0
2	18	0	53	1	0
3	6	1	55	3	0
4	4	0	56	1	0
5	10	0	57	1	1
6	4	0	58	1	0
7	3	0	59	1	1
8	5	1	61	1	0
9	3	1	62	1	0
10	6	1	63	1	0
11	2	0	64	3	0
12	2	0	65	1	0
13	2	1	67	1	0
14	2	0	68	2	1
16	2	1	69	1	0
19	1	0	72	1	1
22	1	0	74	1	0
23	1	0	77	2	2
25	2	2	79	1	0
27	1	0	86	1	0
28	3	1	98	1	0
31	1	0	100	1	1
32	1	0	103	1	1
35	1	0	104	1	0
36	2	1	119	1	1
40	3	0	142	1	1
42	3	0	135	1	1
44	2	0	425	1	1
47	1	0	700	1	1
48	3	0	800	1	1
50	1	0	1000	1	1

The results cannot be considered as entirely convincing in view of the many factors involved in a successful inoculation. The evidence indicates, however, that, as to the minimal number of uredospores which can possibly produce infection, it is possible for a single uredospore to produce infection. In each of the two cases in which infection was produced after inoculation with a single uredospore, the rust appeared after the usual incubation period as a very small pustule at the point of inoculation. In one case the infected leaf withered shortly after the appearance of the pustule; in the other instance the mycelium showed normal growth, and about a week later seven new uredosori were produced in a ring around the first pustule.

As regards the second question, the minimal dose of uredospores which will certainly produce infection, the data indicate this to be, for the conditions under which the work was done, between 100 and 125. This is high. In view of the varying viability of spores taken at one time from the same pustule, and of their further variation with the age of the pustule, it was not considered possible actually to test the germination for each sample used. However, the spores were always taken from the surface of a large and pulverulent sorus, and, considering that the index of germination

of the uredospores under the conditions of inoculation was from 75–90 percent, and that it is possible for a single spore to produce infection, we can say that (taking the conservative germination figure of 50 percent) of more than fifty spores germinating on the surface of the leaf, only one produced successful infection. Evidently, successful infection by a uredospore involves other factors besides that of germination on the leaf surface of the host plant.

The Constitution of the Fungous Mycelium as a Factor in Teleutospore Production by Puccinia coronifera

Our knowledge of the conditions governing teleutospore production in the cereal rusts is summarized and extended by Gassner (1915), who considers that the determining factor is the physiological aging of the host tissue, teleutospore production being particularly coincident with the mobilization of the food resources of the plant for flower and fruit production. The picture of teleutospore production presented by the plants of the experimental field plots described above closely parallels Gassner's observations in similar experiments and is consistent with his views.

Consideration of the behavior of *Puccinia coronifera* as regards teleutospore production, when grown in the greenhouse, leads to the suggestion that the protoplasmic constitution of the fungous mycelium may be a factor. Greenhouse cultures of the rust from material brought in from the field in the vicinity of New York exhibited moderate teleutospore production. A series of cultures from material sent the writer by J. I. Durrell from Ames, Iowa, on the other hand, grown at the same time on similar host material and under similar conditions, showed very abundant teleutospore production, the difference in this respect between the two series of cultures being readily noticeable. While such teleutospore production on potted oat seedlings in the greenhouse is more commonly on the older infected leaves, which are yellowing at the tip, it is not unusual to observe the production of teleutospores by rust pustules on young and vigorous leaves shortly after first infection.

Experiment showed that it is readily possible to secure variation in the tendency of the rust towards teleutospore production by selection. The rust was grown in test tubes under aseptic conditions. Large variation in the tendency towards teleutospore production was noted in cultures of the third generation, some rust cultures showing no teleutosori at all; in others as much as 75 percent of the pustules were teleutosori. Two series of cultures were therefore propagated. In one of the series, transfers were made from cultures showing no teleutospores. Of 36 cultures in this series, 20 showed complete absence of teleutosori; only 2 of the cultures developed more than 50 percent of the winter stage.

In the second series, transfers were made from cultures showing 75 percent teleutosori. Of 35 cultures in this series, 30 showed more than

50 percent teleutosori, and only 5 less than that. Two of the cultures in this series never produced any uredospores whatever, teleutosori only being developed. It was obviously impossible to make transfers from such cultures.

Figure 3, Plate XII, shows a rust mycelium in which only the first pustule produced uredospores, succeeding pustules bearing only teleutospores.

Apparently there may be wide differences in the tendency towards the production of teleutospores in different cultures of a rust fungus, and the factor of fungous constitution should be given consideration in work on the conditions of teleutospore production.

Nutrition and Growth Studies

Water Cultures

Six experiments were performed with *Puccinia Sorghi* on corn to test the effect on rust development of growing the host plants in culture solutions of varying nutritive value. A sugar corn was used, as being more susceptible to rust than a flint or dent corn. The seedlings were grown in water culture in 250-cc. Erlenmeyer flasks. Knop's nutrient solution was used as a base. Except as otherwise noted, the endosperm was removed about the time that the first leaf was breaking through the coleoptile, so that the plant was entirely dependent for sustenance on the mineral salts it could obtain from the nutrient solution and on the carbohydrates it could manufacture in its leaf tissue. Inoculation was effected by spraying with a suspension of uredospores and covering with a bell jar for 24 hours. Observations were made on the incubation period and on the progress of the disease on the plants. The dry weight of the top of the plant at the conclusion of the experiment was taken as an index of the relative vigor of growth of the plant.

TABLE 5

Exp. 1. Effect of Renewing Solution. Plants Inoculated February 28, 1919

No. of Plant	Treatment	Dry Weight of Top of Plant in Mg.	Observations		
			March 9	March 11	March 13
1.....	Solution changed once a week	340	3 pustules on third leaf	1 pustule on second leaf; 3 pustules on third leaf	2 pustules on second leaf; 3 pustules on third leaf
2.....	Solution not changed	310	No infection	1 pustule on second leaf	1 pustule on first leaf; 4 pustules on second leaf; 1 pustule on fourth leaf
3.....	Solution not changed	280	No infection	No infection	1 pustule on first leaf; 1 pustule on third leaf

Exp. 2. Effect of Removing Endosperm. Plants Inoculated February 28, 1919

No. of Plant	Treatment	Dry Weight of Top of Plant in Mg.	Observations			
			March 9	March 11	March 13	March 15
1.....	Endosperm not removed	150	3 pustules on first leaf	4 pustules on first leaf	4 pustules on first leaf	5 pustules on first leaf
2.....	Endosperm removed	80	No infection	1 pustule on second leaf	1 pustule on second leaf	3 pustules on second leaf
3.....	Endosperm removed; solution rendered highly toxic by large excess of Fe_2Cl_6	40	No infection	No infection	No infection	No infection

Exp. 3. Effect of Culture Solutions of Varying Nutritive Value. Plants Inoculated March 19, 1919

No. of Plant	Treatment	Dry Weight of Top of Plant in Mg.	Observations			
			March 25	March 26	March 27	March 29
1.....	Full nutrient solution; endosperm not removed	160	Infection on second and third leaves	Infection on second and third leaves	13 pustules on second leaf; 4 pustules on third leaf	2 pustules on first leaf; 1 pustule on second leaf; 7 pustules on third leaf
2.....	Full nutrient solution	80	No infection	No infection	3 pustules on first leaf; 4 pustules on second leaf	5 pustules on first leaf; 5 pustules on second leaf
3.....	Full nutrient solution	80	No infection	No infection	1 pustule on first leaf; 2 pustules on second leaf; 1 pustule on third leaf	3 pustules on first leaf; 4 pustules on second leaf; 2 pustules on third leaf
4.....	Nutrient solution rendered toxic with excess of Fe_2Cl_6	50	No infection	No infection	2 pustules on second leaf	2 pustules on second leaf; 1 pustule on third leaf
5.....	Tap water	40	No infection	No infection	1 pustule on first leaf; 2 pustules on third leaf	2 pustules on first leaf; 2 pustules on second leaf; 1 pustule on third leaf
6.....	Distilled water	20	No infection	No infection	No infection	2 pustules on second leaf
7.....	Highly toxic nutrient solution	20	No infection	No infection	No infection	1 pustule on first leaf

Exp. 4. Effect of Varying Concentration of Nutrient Solution. Plants Inoculated April 2, 1919

No. of Plant	Concentration of Nutrient Solution	Dry Weight of Top of Plant in Mg.	Observations		
			April 8	April 9	April 14
1.....	0.012	20	No infection	No infection	No infection; plant dying
2.....	0.009	140	Rust showing on second leaf	12 pustules on second leaf	Large number of pustules on first, second, and third leaves
3.....	0.006	110	No infection	3 pustules on second leaf	5 pustules on second leaf; plant dying
4.....	0.003	110	Rust showing on third leaf	19 pustules on second leaf; 10 pustules on third leaf	5 pustules on first leaf; 20 pustules on second leaf; 10 pustules on third leaf
5.....	0.0015	100	No infection	No infection	17 pustules on first leaf; 8 pustules on second leaf
6.....	Distilled water	(destroyed)			

In all the water-culture experiments (table 5) an increase in the incubation period of the rust with depression in the vigor and rate of growth of the host plant was apparent. Coincident with the increased incubation period of the rust on host plants of poor growth and little vigor went always a marked depression in the luxuriance of the fungus. The pustules were appreciably smaller, and produced decidedly fewer spores.

Comparing the incubation period of the rust on the leaves of the same plant, it is found to be shorter on the younger leaves. Comparing the first and second leaves, we find:

Infection noted on the first leaf before it appeared on second leaf....	0
Infection noted simultaneously on first and second leaves...........	5
Infection noted on second leaf before first........................	7
Infection on first leaf; none on second...........................	2
Infection noted on second leaf; none on first......................	7

The older host tissue, it would seem, provided a less congenial environment for the development of the rust.

Incidental to the above-described water-culture experiments was the demonstration of the ability of the rust to develop on chlorotic tissue. Some corn seedlings were grown in iron-free nutrient solution, and the fourth and fifth leaves produced by the plants were completely blanched. The plants were sprayed with a spore suspension to test the susceptibility of these leaves to the rust. Nine days after inoculation the chlorotic leaves showed abundant rust infection. Giddings (personal communication) has obtained infection with *Gymnosporangium juniperi-virginianae* on apple leaves blanched by being kept in the dark room while unfolding from the bud. It may be concluded that the presence of chlorophyll is not a necessary condition for rust development.

Soil Cultures

From the studies of Sheldon, Ward, and Stakman, as also from the experiments described above, it may be considered as established that, within the range of forms worked with, conditions unfavorable to the growth of the host cause an increase in the incubation period of the rust and depress the luxuriance of growth of the fungous mycelium as indicated by the size of the pustules and the number and size of the spores produced in them.

Concerning the effect of conditions unfavorable to the growth of the host on the incidence of rust infection—the number of successful infections produced on a unit area of host tissue by a given dose of inoculum—our knowledge must be regarded as not so definite. The data extant are subject to criticism because of the relatively small number of variables studied and because of the irregularity of dosage inherent in the method of inoculation employed. Ward (1902*b*) applied spores to the leaf by means of a swab of cotton, and Stakman (1914, p. 11) employed a flat inoculating needle for this purpose.

Studies on the relation between host vigor and incidence of infection, to be of critical value, must be made with numbers of variables sufficient to preclude undue distortion of the results by fluctuations in condition of host and fungus, and by errors in the taking and studying of data; the method of inoculation employed must stand criticism as to the uniformity of dosage for the variables compared; and, if any but the grossest relations between the variables studied are to be made apparent, a more exact basis than visual observation and judgment must be employed for determining vigor of growth of host plant and degree of rust infection on it.

In the experiments described below on the relation between host vigor in the oat plant and its susceptibility to crown rust, data were obtained on 1450 individual plants receiving different nutritive treatment and exhibiting wide variation in vigor of growth. The plants were grown in pots in the greenhouse. Inoculation was effected under natural field conditions by placing the pots containing the experimental plants out of doors near a stand of oats heavily infected with crown rust. Analysis of the data indicates that the dosage for the variables compared was uniform. The experiments were concluded and the readings taken before the rust on any of the plants approached the maximum that the leaf tissue could support, so that the infection present at the time may be considered an index of the response of the host tissue to the conditions of inoculation to which it was subjected, and variation in this response between host tissues receiving similar doses of inoculum was presumably due to differences in the condition of the tissues compared.

Values for the vigor of the host plant and for the amount of rust infection present on it were obtained as follows: At the conclusion of the experiment the plant was cut off at the base and observations were taken

of the number of rust pustules on the upper surface of each leaf, of the length of each leaf in inches, of the extreme length of the entire plant, and of the number of stools it had produced. The plant was then dried, and its dry weight was obtained. The dry weight of the plant was adopted as the index of its relative vigor of growth, because more accurate seriation of the variables is possible on this value than on an index such as the height of the plant or the total leaf length.

As an index of the degree of infection of the plant the value adopted was the number of pustules on an average unit area of the most severely infected leaf—calculated by dividing the number of rust pustules on the leaf by the length of the leaf in inches, and by its width at the base in sixteenths of an inch. This value was found to have a positive correlation ($r = .7803 \pm .0167$ for the 250 variables of experiments I, II, and III) with the value that at first thought would seem most desirable: namely, the total number of rust pustules counted on the leaves of the plant, divided by the total leaf length in inches, and by the largest leaf width in sixteenths of an inch—and is preferable for adoption in work of this kind not only because it is easier to obtain, but also because it avoids the error introduced by the development of new leaf surface during the incubation period of the rust. The most highly infected leaf on the plant was usually the lowest leaf in good condition. In tables 6–10 both values are given.

Experiment I

66 oat plants were grown in soil in 2-inch pots, divided into three groups on the basis of the number of plants grown to a pot. The soil was a rich garden loam. The seed was sown July 6, 1920, three grains being put into the soil for every plant desired, and the seedlings were later thinned out to the number of plants desired. The pots were kept on a bench in the greenhouse until August 11, when they were taken out of doors and set near a patch of rusty oats, subjecting the plants to natural conditions of inoculation and infection. The experiment was concluded on August 24. The data on this experiment are given in table 6.

TABLE 6

Group	No. of Variables	No. of Plants to a 2-inch Pot	Mean Dry Weight of Top of Plant in Mg.	Mean No. of Pustules per Ave. Unit Area of Total Leaf Surface	Mean No. of Pustules per Ave. Unit Area of most Severely Infected Leaf
a	23*	5	61	1.1	4.2
b	18	2	135	2.1	6.0
c	25	1	183	2.3	6.1

* Plus 2 destroyed.

Experiment II

70 plants were grown in 3-inch pots, divided into three groups on the basis of the number of plants grown to a pot. Soil, method of seeding, and dates

of sowing, setting out of doors to be inoculated, and of concluding the experiment were the same as in experiment I described above. The results are shown in table 7.

TABLE 7

Group	No. of Variables	No. of Plants to a 3-inch Pot	Mean Dry Weight of Top of Plant in Mg.	Mean No. of Pustules per Ave. Unit Area of Total Leaf Surface	Mean No. of Pustules per Ave. Unit Area of most Severely Infected Leaf
a	25	5	96	1.6	4.1
b	20	2	264	1.7	4.8
c	25	1	407	2.0	5.2

Experiment III

120 plants were grown in $4\frac{1}{2}$-inch pots, divided into four groups on the basis of the number of plants grown to a pot. Soil, method of seeding, and dates of sowing, of setting out-doors to be inoculated, and of concluding the experiment were the same as in experiment I. Results are given in table 8.

TABLE 8

Group	No. of Variables	No. of Plants to a $4\frac{1}{2}$-inch Pot	Mean Dry Weight of Top of Plant in Mg.	Mean No. of Pustules per Ave. Unit Area of Total Leaf Surface	Mean No. of Pustules per Ave. Unit Area of most Severely Infected Leaf
a	50	10	161	1.5	3.6
b	25	5	352	2.4	6.4
c	20	2	661	2.7	6.5
d	25	1	976	2.5	6.2

Experiment IV

600 oat plants were grown in $4\frac{1}{2}$-inch pots, 5 plants to a pot; 15 grains being planted in each pot in the first place, and the young seedlings thinned out to the desired number. The plants were divided into six groups of 100 individuals each on the basis of soil composition and treatment, as follows:

Group A: Soil composed of sand only.

Group B: Soil a mixture of $\frac{4}{5}$ sand and $\frac{1}{5}$ garden loam.

Group C: Soil a mixture of $\frac{1}{2}$ sand and $\frac{1}{2}$ garden loam.

Group D: Soil the same mixture as in Group C. In addition, KCl at the rate of 350 pounds to the 6-inch acre of 2,000,000 pounds was intimately mixed with the soil.

Group E: Soil the same mixture as in Group C. In addition, acid phosphate at the rate of 750 pounds to the acre was intimately mixed with the soil.

Group F: Soil the same mixture as in Group C. In addition, sodium nitrate at the rate of 500 pounds to the acre was intimately mixed with the soil.

Seed was sown July 11, 1920. On July 24, July 31, and August 7 the plants of groups *D*, *E*, and *F* had additional quantities of fertilizer applied

in water solution at the rate of 100 pounds to the acre. On August 9 the plants were placed out of doors to be inoculated. The experiment was concluded on August 27. Figures 1 and 2, Plate XI, illustrate the growth differences obtained between the plants of the different groups in these experiments.

In table 9, the groups are arranged in order of the vigor of growth exhibited by the plants.

TABLE 9

Group	No. of Variables	Soil Treatment	Mean Dry Weight of Top of Plant in Mg.	Mean No. of Pustules per Ave. Unit Area of Total Leaf Surface	Mean No. of Pustules per Ave. Unit Area of most Severely Infected Leaf
A	100	sand	120	.6	2.0
E	100	acid phosphate	155	.8	2.7
B	100	$\frac{4}{5}$ sand	200	.7	2.3
D	100	KCl	202	1.0	3.2
C	100	$\frac{1}{2}$ sand	341	.9	3.1
F	100	$NaNO_3$	564	1.2	4.5

Experiment V

This was a duplicate of Experiment IV, started a week later. The seed was sown July 17, the plants were placed out of doors to be inoculated August 10, and the experiment was concluded August 31. The results are shown in table 10.

TABLE 10

Group	No. of Variables	Soil Treatment	Mean Dry Weight of Top of Plant in Mg.	Mean No. of Pustules per Ave. Unit Area of Total Leaf Surface	Mean No. of Pustules per Ave. Unit Area of most Severely Infected Leaf
A	100	sand	47	5.1	11.6
B	100	$\frac{4}{5}$ sand	53	5.1	11.8
E	100	acid phosphate	93	5.2	11.3
C	100	$\frac{1}{2}$ sand	93	4.5	9.5
D	100	KCl	96	4.4	10.2
F	100	$NaNO_3$	359	3.1	7.6

Relation between Host Vigor and Pustule Size

In all five of the soil-culture experiments there was evident a marked decrease in the size of the rust pustules on the host plants the growth rate of which was depressed. The lengths of 100 contiguous pustules on plants from groups *a* and *c* of experiment I; groups *a* and *c* of experiment II; groups *a* and *d* of experiment III; groups *A* and *F* of experiment IV; and groups *A* and *F* of experiment V were found to fall into the classes shown in table 11.

TABLE II

	Experiment									
	I		II		III		IV		V	
	Group		Group		Group		Group		Group	
	a	*c*	*a*	*c*	*a*	*d*	*A*	*F*	*A*	*F*
No. of pustules ½ mm. long......	94	20	72	14	82	22	96	12	70	8
" " " 1 mm. "	6	20	28	34	18	30	4	30	25	24
" " " 1½ mm. "		34		38		30		46	3	24
" " " 2 mm. "		24		8		12		8	2	34
" " " 2½ mm. "		2		4		4		4		7
" " " 3 mm. "				2		2				3
Sum of lengths of 100 pustules in mm.	53	134	64	130	59	126	52	131	68	169

Figures 4 and 5 of Plate XII illustrate the relative size of the pustules on leaves of semi-starved and of vigorously growing plants.

Pustules attained a larger size on the more rapidly growing host plants, indicating that a more luxuriant host tissue means a more luxuriant parasitic mycelium.

DISCUSSION

Relation between Host Vigor and Incidence of Infection

On their face the figures obtained in the soil-culture experiments indicate that in experiments I, II, III, and IV there occurred a decreased incidence of infection with depression in growth vigor of the host; but in experiment V the figures indicate quite as definitely precisely the opposite relation—namely, increased incidence of infection with depression in the growth rate of the host.

The dosage for all six groups of variables in soil-culture experiments IV and V was probably essentially the same. The plants were arranged in order of alphabetical designation of the groups: *A*, *B*, *C*, *D*, *E*, *F*. The possibility might be suggested that in experiment IV inoculation proceeded from the direction of *F* and that the plants from *F* to *A* were subjected to progressively diminishing doses of inoculum; and, conversely, that in experiment V inoculation was from the direction of *A* and that the plants from *A* to *F* received progressively diminishing doses of uredospores. This would make the amount of infection observed on the plants of the different groups a function of their positions relative to each other. But actually the amount of infection observed is correlated not with the position of the group but with its relative growth vigor as indicated by the mean dry weight of the plants. Thus, in both experiments IV and V, group *E* exhibits an amount of infection not like group *F*, next to which it was placed, but like group *B* which it resembles in vigor of growth. We may conclude that

the dosage for the variables compared in any experiment was uniform and that the variation in the amount of rust observed on the different groups of plants in the experiment is due to differences in the reactions of the plant tissue to the infection to which they were subject.

The explanation of the apparent reversal of the result in soil-culture experiment V as compared with the others is probably to be found in the age of the plants and in the length of time they were exposed to infection. The experiments are compared in table 12.

TABLE 12

Experiment	I	II	III	IV	V
Age of plants at conclusion of experiment (days)	49	49	49	47	45
Age of plants when set out of doors to be inoculated	35	35	35	31	24
Number of days out of doors and exposed to infection	15	15	15	16	21
Number of variables	66	70	120	600	600
Average dry weight of top of plants (mg.)	127	278	538	264	123
Average infection (total leaf surface)	1.8	1.8	2.3	.9	4.6
Average infection (most severely infected leaf)	5.4	4.7	5.7	3.0	10.4

Experiment V differs from the other four experiments in that (1) when set out of doors to be inoculated the plants were from 7 to 11 days younger. Even at the conclusion of the experiment these plants had only half the dry weight of the plants of experiment IV and were evidently much less mature. (2) When the experiment was concluded the plants had been out of doors and subject to infection 6 days longer. If we allow an incubation period of 10 days for the rust, then the rust present on the plants of experiment V at the conclusion of the experiment represents inoculation through a period of time twice as long as in the case of the other experiments. (3) The amount of rust on the plants at the conclusion of the experiment was several times greater in experiment V than in any of the other experiments.

The last-mentioned fact immediately brings into view an aspect of the method of experimentation used tending to limit the value of the pustule count as a criterion of the frequency of penetration and infection by the uredospore germ tube. It is probable that only in cases of very sparse infection is there a pustule for every focus of infection, and that only in cases of very sparse infection is the number of pustules counted an accurate index of the number of infections which have taken place. With abundance of infection there appears a tendency for the coalescence of foci of infection, for two or more mycelia the result of contiguous infections to coalesce and produce only one pustule; and this tendency would be highly accentuated on the more vigorously growing host plants where the parasite finds a favorable nidus and develops more luxuriantly. In experiment V the error introduced by the coalescence of mycelia may well have masked a

higher incidence of infection in the vigorously growing plants of group *F* and have converted it into an apparently lower susceptibility. It is noticeable that the pustules were larger in experiment V than in the other four experiments.

Variation in the Incidence of Rust Infection with Variation in the Growth Vigor of the Host Plant, due to Constitutional or Racial Differences

In soil-culture experiments IV and V, when the 100 variables of each group were arranged in the order of their dry weight, the series divided into five equal parts of 20 variables each, and the average weights and degrees of infection of these sub-groups determined, a certain relation was apparent between the relative weight attained by a plant and the incidence of rust infection on it. The figures obtained in this analysis of the data are presented in table 13.

TABLE 13

Experiment IV

Group	Mean Dry Weight of Tops of Plants in Mg.					Mean Infection per Unit Area of most Severely Infected Leaf of Plant				
	Sub-groups									
	First	Second	Third	Fourth	Fifth	First	Second	Third	Fourth	Fifth
A....	40	65	110	148	239	2.3	2.4	1.8	2.0	1.6
E....	99	129	148	172	231	2.8	2.1	2.9	3.5	2.1
B....	99	140	179	231	345	2.3	2.9	2.5	2.1	1.8
D....	90	144	182	231	363	3.6	3.0	2.5	3.9	2.9
C....	141	233	336	430	596	4.0	3.0	2.3	4.4	1.7
F....	305	450	555	653	812	4.7	5.7	5.2	3.8	3.3
	129	193	252	311	431	3.3	3.2	2.9	3.3	2.2

Experiment V

Group	Mean Dry Weight of Tops of Plants in Mg.					Mean Infection per Unit Area of most Severely Infected Leaf of Plant				
	Sub-groups									
	First	Second	Third	Fourth	Fifth	First	Second	Third	Fourth	Fifth
A....	21	34	43	54	83	11.8	13.6	11.5	11.6	9.3
B....	22	36	50	65	92	12.3	14.0	11.7	12.2	8.6
E....	42	67	85	108	159	15.9	12.2	11.9	8.6	7.8
C....	53	71	88	106	148	10.2	10.0	11.0	8.6	7.4
D....	47	72	90	107	162	12.0	13.2	10.5	8.0	7.2
F....	190	283	349	416	558	9.9	6.8	7.2	7.7	6.2
	63	94	118	143	200	12.0	11.6	10.6	9.5	7.8

The figures show that there was considerable variation in the growth

attained by plants receiving the same treatment, and that the larger plants were less susceptible to rust infection—increased resistance being particularly marked in the sub-group including the largest of the plants.

The seed employed was a commercial "Swedish Select" oats in which we should expect a mixture of strains as regards rate of growth, speed of maturity, and susceptibility to rust. In view of the uncertainty as to the varietal purity of the seed employed, the differences in incidence of rust infection on plants receiving the same treatment and showing differences in vigor of growth are probably indicative of constitutional differences in susceptibility to rust which may be correlated with similar constitutional differences in speed of growth; and so may be considered as not necessarily bearing on the main problem I am considering, which is concerned with the effect on rust susceptibility of externally induced variations in the vegetative vigor of the host. The establishment of an inverse relation between susceptibility to rust and speed of growth in oat varieties would, however, lend new significance to the practical injunction of the agronomists to plant early-maturing varieties of oats in order to escape loss from rust, indicating that selection of rapidly growing and early-maturing strains of oats automatically implies selection for rust resistance as well.

The Possibility of a Direct Relation between Environmental Conditions and Rust Resistance

Groups *D*, *E*, and *F* in experiments IV and V were intended as tests for a possible direct effect on rust susceptibility of specific nutrient substances—that is, an effect independent of variations in the health and vigor of the host plant. A potash fertilizer was applied to the plants of group *D*; a phosphate fertilizer to those of group *E*; and the plants of group *F* were richly fed with a nitrogen salt.

The infection observed in these groups is in no instance so far different from that on plants of similar weight in the groups not treated with any special fertilizer as to justify the inference that the fertilizing chemicals were exerting any influence on the rust resistance of the host other than is implied in their effect on the general condition and vigor of the plant.

In experiment IV the potash and phosphate applications proved excessive, and the growth of the plants was appreciably retarded as compared with the plants of group *C*; in experiment V the potash and phosphate fertilizers had no effect on the growth of the plants. In both experiments the potash- and phosphate-fertilized plants show a somewhat higher incidence of infection than plants of similar weight not treated with special fertilizers; a tendency at variance with the statements of Bolley (1889, p. 18) and Spinks (1913, p. 247) that these fertilizers give increased rust resistance. In group *F* the stimulating action of the nitrate fertilizers on the growth of the host was so marked that there can be no hesitation in referring the increased susceptibility observed to this effect rather than to any direct

action of the chemical. This aspect of the soil-culture experiments may be considered as in agreement with the suggestion arrived at in the bibliographical review that it is questionable whether a direct relation between any environmental factor, either physical or chemical, of the nature of a nutrient or a stimulus, and susceptibility to rust, has been established in the case of the cereal grains.

Vegetative Vigor of the Host as a Susceptibility- and Resistance-factor in Infectious Diseases

Increased susceptibility with increased vigor of the host, in plant diseases, is not confined to the rusts. Marchal (1902) found that infection of lettuce by *Bremia lactucae* was favored by nitrogen and phosphates and retarded by an excess of potash. Jones (1905, p. 38) mentions that high fertilization, especially with nitrogenous manures, lowers the powers of the potato plant to resist blight and rot. McCue (1913, p. 18) observed that tomato plants treated with phosphatic fertilizers developed less leaf blight than control plants, while plants on nitrogen and potash plots which at the same time gave the highest yields, indicating greatest vigor of growth, were more heavily infected than the controls. Peltier (1918) has observed with the citrus canker, and Fromme and Murray (1919, p. 227) with the angular leaf spot of tobacco ("the development of the organism within the tobacco leaf is apparently dependent to a marked degree on those predisposing factors which promote a rapid, vigorous growth of the host"), that infection is heavier under conditions which favor the growth of the host. Thomas (1921) obtained evidence of increased resistance to leaf spot (*Septoria Apii*) of celery plants the vitality of which was depressed as a result of infestation of the root system by nematodes; and of decreased resistance in plants richly fed. And Levine (1921) has observed that crown gall on beets developed more rapidly and to larger size on roots grown in a highly manured soil.

While the claim that increased vigor of the host means greater susceptibility to an infection may appear somewhat anomalous from the point of view of current theories regarding the infectious diseases, observations such as form the subject of the present paper are readily understood when we consider the infectious diseases in the light of the larger class of biological phenomena of which they are an artificially selected group—namely, parasitism, commensalism, and symbiosis, the class of biological phenomena in which one organism lives within, and derives its sustenance from, the tissues of another living organism. In each of the four main groups of parasitic organisms—the bacteria, the protozoa, the worms, and the fungi—a series of intergradations are to be observed in the physiological interrelations of host and parasite, from the unceasing and violent struggle that continues until the destruction of one or other of the principals, to a relation of a more benign type characterized by great subordination and even tend-

ency to usefulness on the part of the parasitic organism, and by the utmost tolerance on the part of the host. In many instances the nature of the reaction is not constant, but varies with the progress of the host-parasite relation. In this intergrading series of possible host-parasite relations, the inverse relation between host vigor and parasite virulence obtains only in the instances and phases where the reaction of the host to the parasite is one of active antagonism; here a more vigorous host means a host of greater physiological capacity to combat the progress of the invader. But when the relation between host and parasite is of a symbiotic type, a more vigorous host means a host in which more food is available for the development of the parasite. Because, of the general class of parasitological phenomena, the instances mainly in the field of pathological interest (the diseases ordinarily so called) are an artificially selected group in which relations of violent antagonism between host and invading organism are most prominently in evidence, thought in the field of pathology has developed with the physiological antagonism of host and parasite as its basal concept; and the theories of immunity extant are largely concerned with the nature of the antagonistic reactions.

In the group of the fungi the transition from violent and destructive parasitism to parasitism of the symbiotic type is accompanied by a transition from facultative to obligate parasitism, as if the physiological corollary of parasitism of the latter type is extreme specialization in food preferences. The series in the fungi grades from violent and destructive parasites like Botrytis, on the one hand, to, on the other hand, so benign an infestation as the seed fungus of *Lolium temulentum* (described by Freeman, 1903) in which the relation is so intimate and devoid of any untoward effect on the host, and the life history of the cohabiting organism is so parallel with that of the grass, that its distinct individuality is almost open to question.

The mutualistic nature of the relation between host elements and fungus in rusts of the type of the cereal rusts is commented on by Tubeuf (1897, p. 91) who very aptly compares the mass of chlorophyll-bearing leaf cells infested with the rust mycelium to a lichen structure, especially to those lichens whose algae obtain water and inorganic materials direct, rather than through the fungous hyphae. Certainly, during the greater part of the relation, there is here no evidence of any deleterious effects on the host cells. While the contribution of the affected elements to the growth and fruiting economy of the host plant as a whole may be diminished, the infected protoplasts continue essentially unimpaired in structure and function. The parasite does not attack the living substance of the host protoplast, but confines itself to establishing such a relation with the latter that it shares the available food resources of the cell; and the rust haustorium is not an implement for mechanical disruption, but a structure more in the nature of the placenta of the mammalian foetus for establishing physiological communication with the food resources of the host.

The data presented by Thomas (1921) on the parallel relation between health of the host and infection in the case of the leaf blight of celery, and observations of similar occurrences in other diseases caused by non-obligate parasites like the late blight of the potato (Jones, 1905) and the crown gall of the beet (Levine, 1921) indicate that phases in which a symbiotic tendency comes to the fore may occur in diseases of a predominantly destructive type caused by facultative parasites, and suggests the generalization that the host-parasite relation in any given instance is not constant but may vary with the state and condition of the organisms and with the progress of the relation. It is important to recognize that there may occur mutualistic phases and stages in host-parasite relations of a violent and destructive type, just as there are destructive phases in parasitisms of a predominantly symbiotic tendency such as those of the mildews, the rusts, and the smuts.

Conclusion

The inquiry initiated by the occurrence in rust literature of statements of a relation between host vigor and susceptibility other than the inverse relation commonly conceived as existing between these variables can be considered as having brought forward evidence indicating that through most of the course of certain infectious diseases such as the rust diseases of the cereal grains, and in certain phases of other diseases like the leaf spot of celery and the crown gall of the beet, the vegetative vigor of the host and the virulence of the disease may be in direct relation. The demonstration of such a relation in diseases of large importance suggests, in turn, emendation of current pathological concepts of the relation between host vigor and pathogen activity into a form more in accord with our knowledge of parasitological phenomena in general. A more catholic point of view in pathologic thought, recognizing that, for longer or shorter phases in the course of a disease, the relation between host and parasite may be highly mutualistic, would be of material value as a working concept in the study of disease and in defining the practical problem of disease prevention and control.

The work presented in this paper was done in the Botanical Laboratory of Columbia University, under Professor R. A. Harper, to whom the writer is greatly indebted for pointing out the problem and for constant consultation and advice during the progress of the investigations. Acknowledgment is also made of indebtedness to Dr. Michael Levine for taking the photographs of the soil-culture experiments, and to Dr. H. E. Thomas for helpful advice in devising the method used in the dosage studies on the corn rust.

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DESCRIPTION OF PLATES

Plate XI

Fig. 1. View of one of the four series of pots of experiment V of the soil-culture studies, illustrating the difference in vigor of growth between plants receiving different nutritive treatment.

Fig. 2. On the left, a pot containing 5 plants of group *A* (grown in sand); and on the right a pot containing 5 plants of group *F* (soil highly fertilized with $NaNO_3$); experiment V of the soil-culture studies.

Plate XII

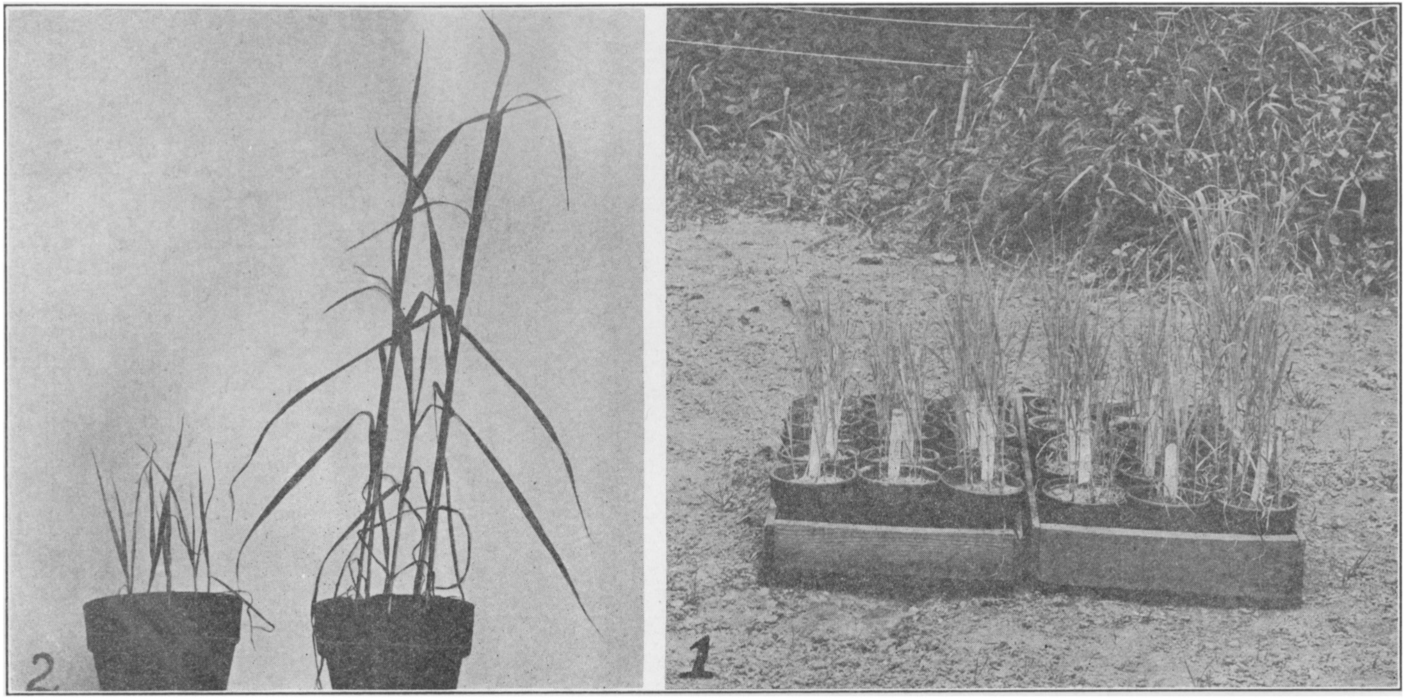
Fig. 3. Crown rust of oats. A rust mycelium exhibiting a very marked tendency towards teleutospore production. The first sorus produced by the mycelium (in the center) is a uredosorus. The others are teleutosori. Photographed with Zeiss 3.5 cm. microplanar. × 24.

Fig. 4. View of infected leaves of a semi-starved plant and of a richly fed plant of soil-culture experiment V, showing larger size of pustules on more luxuriant host plant. Photographed with Zeiss microplanar. × 15.

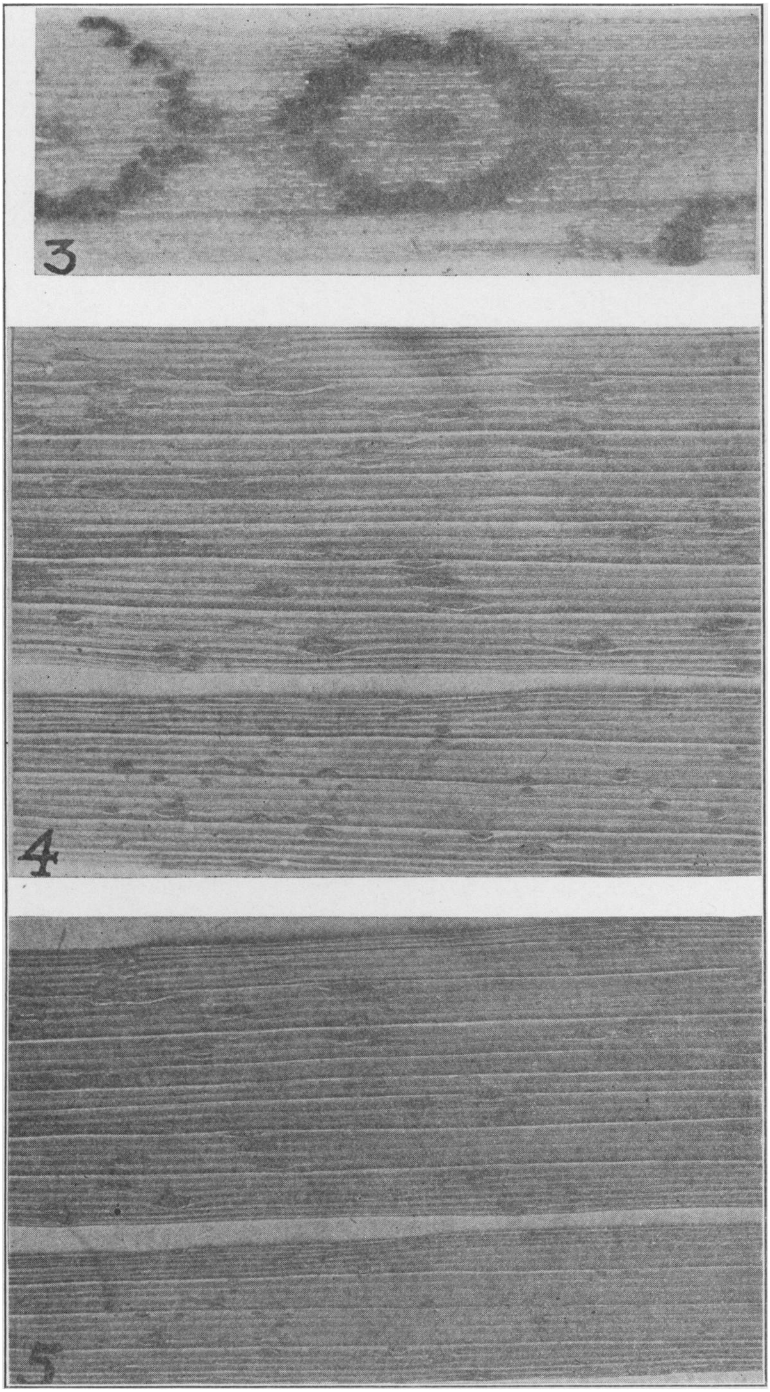
Fig. 5. Same as figure 4. × 10.

Erratum

In the first part of this paper, appearing in the **Journal** for April, 1922, pp. 183–203, on page 188, line 32, and on page 193, line 1, for *Puccinia Caryophylli* read *Uromyces caryophyllinus*.



RAINES: VEGETATIVE VIGOR OF THE HOST



RAINES: VEGETATIVE VIGOR OF THE HOST